

A REVIEW OF NESTING BEHAVIOR IN THE
GENUS *ENTOMOGNATHUS*, WITH NOTES ON
E. MEMORIALIS BANKS
(HYMENOPTERA: SPHECIDAE)

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The genus *Entomognathus* contains at least 40 species, half in the Ethiopian and in the Palaearctic, Nearctic, Oriental, and Neotropical regions (Leclercq, 1954, 1955, 1961, 1963; Nouvel and Ribaut, 1956; Krombein, 1963). Relatively little is known about the nesting behaviors, host preferences, or life histories of members of this genus. Only the Palaearctic *E. (Entomognathus) brevis* van der Linden has been studied in any detail, and almost nothing is known about the four U. S. species belonging to the subgenus *Toncahua*. One of the purposes of the present paper is, therefore, to amalgamate information on the host preferences, nesting behaviors, life histories, and immature stages of the species of *Entomognathus*, based upon a review of the world literature. The major portion of this paper details the components of the nesting behavior of *E. (Toncahua) memorialis* Banks, describes the mature larva and cocoon, and compares this species and related crabronine and larrine wasps in nesting ethology and larval and cocoon morphology. The adult wasps and prey beetles have been placed in the S. U. N. Y. College of Forestry Insect Museum, and the mature larva has been deposited in the Museum of Comparative Zoology, Harvard University.

Entomognathus (Mashona) mimicus Arnold

One female from Bekily, Madagascar was observed by Arnold (1944) preying upon a small chrysomelid beetle.

Entomognathus (Mashona) patricius Arnold

Arnold (1932) reported several females nesting in a clay bank beside a stream in Bulawayo, S. Rhodesia. The wasps were preying upon a species near *Ootheca modesta* Gahan (Chrysomelidae: Galeucinae).

Entomognathus (Entomognathus) brevis v. d. Lind.

This widely distributed Palaearctic species has been reported to nest in sand, gravel, clay, and chalky-loam, and to burrow in hori-

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Manuscript received by the editor July 5, 1972.

zontal and vertical situations as well as in depressions (Chambers, 1949). *E. brevis* has been known to nest in or near woodlands (Grandi, 1927; Chambers, 1949), and to aggregate (Benoist, 1915). According to Adlerz (1912), females were observed to enter the burrows of other wasps, remain for only a moment, and exit, but it was not ascertained whether the wasps used pre-existing burrows for nest-sites.

The females have been noted to construct earthen, chimney-like extensions of the burrows, 10-25-mm-long, above the ground surface (Benoist, 1915; Grandi, 1927, 1931), or to make no such extensions (Maneval, 1928, 1937; Abrahamsen, 1951). Grandi (1931) found nests with and without turrets in the same area. The main burrow, 2-3 mm in diameter, plunged obliquely downward, sometimes circumventing subterranean obstacles, and at depths of 6-12 cm branched into side burrows leading to the cells; the oval cells, 4 × 8 mm, were located at depths of 6-12 cm beneath the surface (Grandi, 1927; Maneval, 1928; Abrahamsen, 1951), the maximum number per nest being ten (Benoist, 1915).

The wasps transported their prey in flight, holding it with the middle legs, and hovered back and forth in front of the entrance before diving inside (Adlerz, 1912).

Seven genera and seventeen species of Chrysomelidae have been reported as prey of *E. brevis* (Table 1). All are members of the subfamily Alticinae except *Cryptocephalus labiatus* L. (Cryptocephalinae). In one of the earliest reports on this species, Sickmann (1893) recorded small flies as prey; however, this record was probably based upon a misidentification of the wasp. The prey are never killed by the wasp but invariably paralyzed (Benoist, 1915; Grandi, 1927, 1931; Maneval, 1928; Abrahamsen, 1951).

Both Maneval (1928) and Grandi (1931) noted that large and small chrysomelids were captured by the wasps. The number of prey stored per cell ranged from 14 to 24. From one to four genera and species were stored in a single cell, and at least two and usually three or four species were captured at all but one of the several localities where more than one prey was collected (Benoist, 1915; Hamm and Richards, 1926; Grandi, 1927, 1931; Maneval, 1928, 1937; Richards, 1944; Abrahamsen, 1951).

According to Grandi (1927) and Maneval (1928), the wasp did not lay her egg until the full complement of prey had been put in the cell. Maneval (1937) found prey near the bottom of the nest in a section of the burrow, 3-4-cm-long, but he did not note an egg attached to any of the beetles. In fully-provisioned cells, the beetles

TABLE 1. Species of prey of *Entomognathus brevis*.

Genus and species of prey	Source
<i>Aphthona euphorbiae</i> Schrank	Grandi, 1931
<i>Aphthona herbigrada</i> Curtis	Grandi, 1927; Maneval, 1937
<i>Aphthona pygmaea nigella</i> Kutsch.	Grandi, 1931
<i>Chaetocnema arida</i> Foudras	Maneval, 1937
<i>Chaetocnema concinna</i> Marsham	Richards, 1944
<i>Chaetocnema hortensis</i> Geoffroy (= <i>aridella</i> Paykull)	Grandi, 1931; Richards, 1944; Abrahamsen, 1951
<i>Chalcoides aurata</i> Marsham	Richards, 1944
<i>Crepidodera ferruginea</i> Scopoli	Maneval, 1928; Bouwman, 1930; Grandi, 1931; Chambers, 1949; Abrahamsen, 1951
<i>Cryptocephalus labiatus</i> Linnaeus	Hamm and Richards, 1926
<i>Longitarsus jacobaeae</i> Waterhouse	Hamm and Richards, 1926
<i>Longitarsus luridus</i> Scopoli	Adlerz, 1912
<i>Longitarsus nasturtii</i> Fabricius	Abrahamsen, 1951
<i>Longitarsus pellucidus</i> Foudras	Grandi, 1927
<i>Longitarsus pratensis</i> Panzer	Grandi, 1927, 1931; Maneval, 1937
<i>Longitarsus succineus</i> Foudras	Maneval, 1928; Grandi, 1931
<i>Longitarsus suturalis</i> Marsham	Maneval, 1937
<i>Phyllotreta nigripes</i> Fabricius	Grandi, 1931
<i>Phyllotreta</i> sp.	Benoist, 1915

were piled indiscriminately with the egg-bearer, ventral-side-upward, on top of the pile; the wasp's egg was attached to the venter of the beetle at the mesal base of the forecoxa, and extended transversely beyond the side of the beetle (Grandi, 1927). It was elongate, subcylindrical, curved, and measured $2 \times \frac{3}{4}$ mm.

The cocoon of *E. brevis* has been reported to be thin-walled and to measure $4.5-6 \times 2-3$ mm (Benoist, 1915). According to this author, the mature larva pushed the uneaten prey fragments to one end of the cell rather than distributing them over the surface of the cocoon. The larva pupated in June of the following year and the adult appeared during the second half of July. Adult wasps have been collected in Europe from the second week in June (Chambers, 1949) to the second week in September (Grandi, 1927).

Entomognathus (Toncahua) texana Cresson

Cazier and Mortenson (1965) collected one female flying above



Fig. 1. Nesting-site of *E. memorialis* Banks at Chittenango, N. Y. Individual nests occupied the upper portion of cliff, among roots.

a sandy river bed in New Mexico with a *Diabrotica tricincta* Say (Chrysomelidae: Galerucinae).

Entomognathus (Toncahua) memorialis Banks

Ecology. Krombein (1963) characterized this species as a sylvicolous form which nests in rather heavy soil. He recorded specimens from Connecticut, New Jersey, Maryland, District of Columbia, Virginia, and Kansas. We observed small aggregations of this species flying near the tops of 1-6-ft-high sand cliffs at Chittenango, Madison Co., N. Y. (Fig. 1) during 19-28 August 1970 and 12 July 1971, and at Presque Isle St. Pk., Erie Co., Pa. from 4 to 9 July 1971. Both sites bordered bulldozed sandy fields near stands of deciduous northern hardwoods. At Chittenango, other sphecids nesting in the cliff included *Philanthus politus* Say, *Oxybelus bipunctatus* Oliv., *O. emarginatus* Say, and *Xylocelia* sp. Cliff-nesting sphecids at Presque Isle comprised *Miscophus americanus* Fox, *Philanthus gibbosus* (F.), and *Xylocelia franclemonti* Krom.

Mating Behavior. Ten males and three females were observed flying in front of the sand cliff at Presque Isle during the 6-day observation period. The males continuously circled a small *Rubus* plant at the base of the cliff and attempted to mate with small

wasps, flies, and beetles as they landed on the leaves. They pursued females in flight and pounced upon them as they rested on the vegetation. One "mating ball" of three males and a female was seen tumbling over the sand until only one male remained whereupon the pair flew, still coupled, into the dense vegetation behind the cliff.

Nest-Site Selection. Although both males and females spent the night in pre-existing holes in the cliff, facing head-outward, these burrows were not utilized by the wasps for nest-sites. The females emerged from the holes between 10 and 11 a.m. and reentered them for the night between 2:30 and 3:30 p.m. The males were seen outside earlier in the morning and later in the afternoon than this. During the day females flew from one preexisting cavity to another, searching longest in root-shrouded areas near the top of the cliff. Occasionally, they climbed up the rootlets and sampled the soil with their mandibles. The males, on the other hand, investigated holes in the cliff only during late afternoon when they were looking for places to spend the night.

At Presque Isle females were out for nearly a week without one of them selecting a permanent nest-site or bringing in provisions. Seven males and three females observed at Chittenango on 12 July 1971 behaved similar to the wasps at Presque Isle, except for one female which entered a nest with prey.

Nest Structure. Seven nests of *E. memorialis* were excavated and studied at Chittenango. The entrances, 4.0-4.5 mm in diameter, were located among dense rootlets, 9.5-24.0 (mean 13.3) cm below the top of the cliff. A narrow, rather inconspicuous streak of sand extended down the slope beneath each entrance, indicating evidence of recent soil removal. The burrows, 3 mm in diameter, entered the outer sandy-loam at about right angles to the cliff and usually arched upward before descending into hard-packed sand in one or more undulations (Fig. 2a-d). The mean length of unobstructed burrow from the entrance was 16.8 (9.5-27.0) cm. The distance from the entrance to the farthest cell in the nest via the burrow ranged from 9.5 to 29.0 (mean 21.2) cm.

The four nests containing the largest number of cells (9-20) exhibited branching of the main burrow. The cells were arranged either singly, in fan-shaped clusters, or in series, with cells in tandem especially common. Tunnels from the main burrow to cells in clusters were not traceable, but those leading to and adjoining the cells in tandem were often loosely filled with sand and easily followed. The broadly oval cells averaged 4.4×8.5 mm and ranged from 4×6 to 5×13 mm ($N=29$). They were located 13.5-25.0

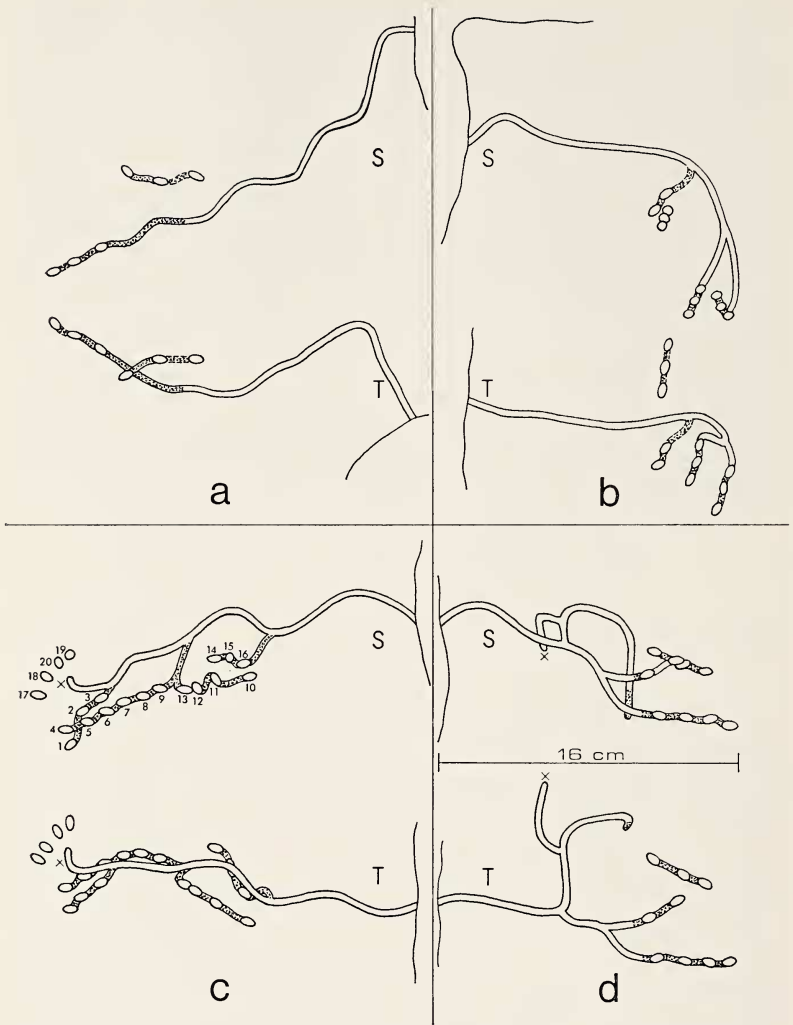


Fig. 2a-d. Side (S) and top (T) views of four nests of *E. memorialis* Banks; x indicates burrow storage, numbers in (c) the sequence in which cells were provisioned. Stippling refers to sand fill. Scale for nest (d) applies to all nests.

(mean 18.8, $N=74$) cm below the top of the cliff. Relative to the entrance, the cells were found from 2.5 cm above its level to 13.5 cm below it, averaging 5.5 cm below. The horizontal distance from the cliff face to a cell averaged 12.2 (4.5-21.5, $N=66$) cm.

The number of cells per nest ranged from 3 to 20 (mean 10.7). Except for cells in tandem, there was no correlation between the age of the cell and its position in the nest. In each tandem series, the cell farthest from the entrance in terms of total burrow length was the oldest. Because cells in series occasionally curved back toward the entrance, an older cell was sometimes closer to the entrance than a newer one in absolute distance (Fig. 2b, c). In nests 1 and 2 (Fig. 2a, b), the female moved farther away from the entrance as she constructed new series of cells. In nest 3 (Fig. 2c), worked on by two females in succession, the first wasp apparently constructed tandem series toward the entrance whereas the second one built a series of three cells near the front and then a fan-shaped cluster of four cells at the back.

Transport and Storage of Prey. A provisioning female returned to her nest in flight, holding the beetle head-forward and venter-up with the middle legs. She usually hovered briefly in front of the cliff face before diving into the open entrance. The myriad of rootlets frequently made entry difficult and may have been responsible for many of the abandoned prey found beneath the entrances.

The single hunting time recorded was 3 min. 15 sec. The same female twice took 2 min. to store a prey and return to the entrance. Temporary storage of beetles in the burrow at some distance from the entrance was recorded for three of the seven nests (Fig. 2c, d). Such prey were placed head-inward and were loosely covered with sand particles. All of the beetles were partially paralyzed and moved their antennae and legs or flexed their elytra.

Nest provisions. Prey taken from the Chittenango nests in 1970 were determined as *Altica ulmi* Woods (Chrysomelidae: Alticinae). Two specimens collected from nests at this locality in July and August 1971 proved also to be this species. E. J. Kurczewski (correspondence) took a *memoralis* female with *A. marevagans* Horn at Presque Isle in August 1971. Of the 220 *A. ulmi* preserved for identification, 46.8% were females and 53.2% males.

The mean number of prey per cell was 5.1 (3-9, $N=42$). The total weight of the beetles per cell in 13 fully-provisioned cells ranged from 16.8 to 54.5 (mean 27.0) mg. Individual beetles weighed from 3.7 to 8.0 (mean 5.4, $N=68$) mg, whereas one female wasp weighed 7.0 mg. The beetles in the cells were positioned head-

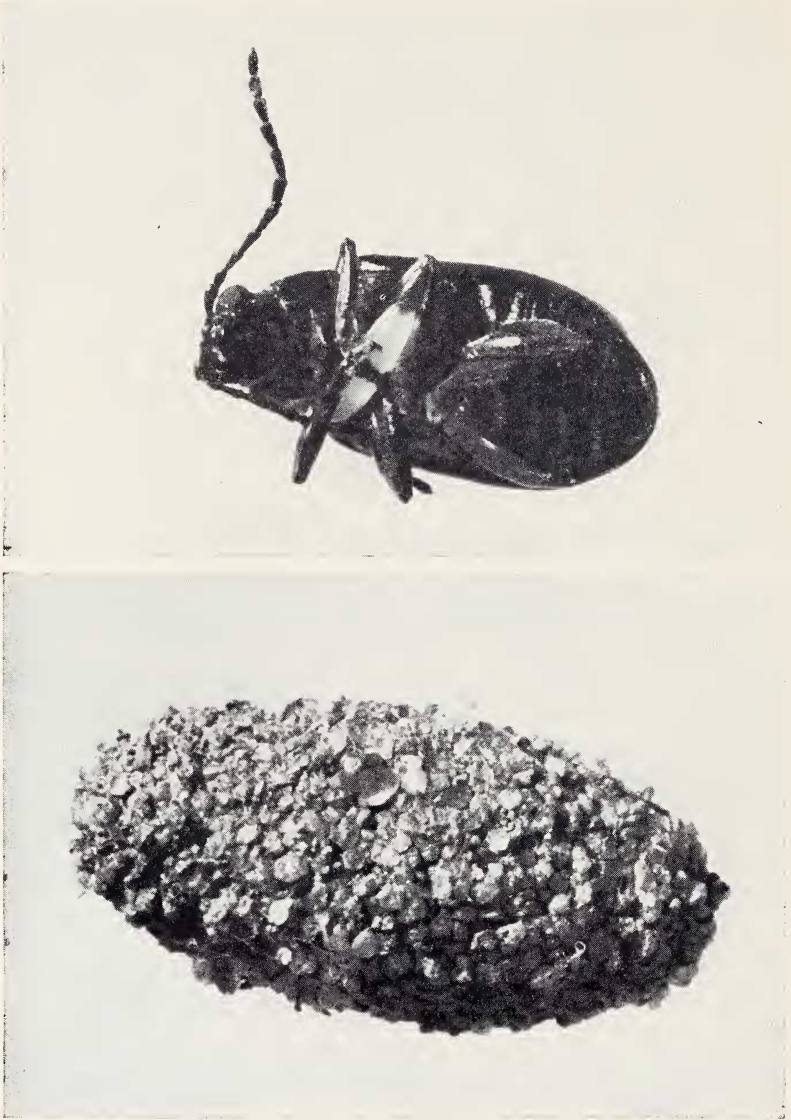


Fig. 3. (above). ♂ *Altica ulmi* Woods bearing egg of *E. memorialis* Banks in typical position.

Fig. 4. (below). Cocoon of *E. memorialis* Banks.

inward and ventral-side-upward or, less commonly, dorsal-side-upward or on the side. The egg-bearing beetle was located at the back end of the cell and was placed venter-up or pressed obliquely against the wall.

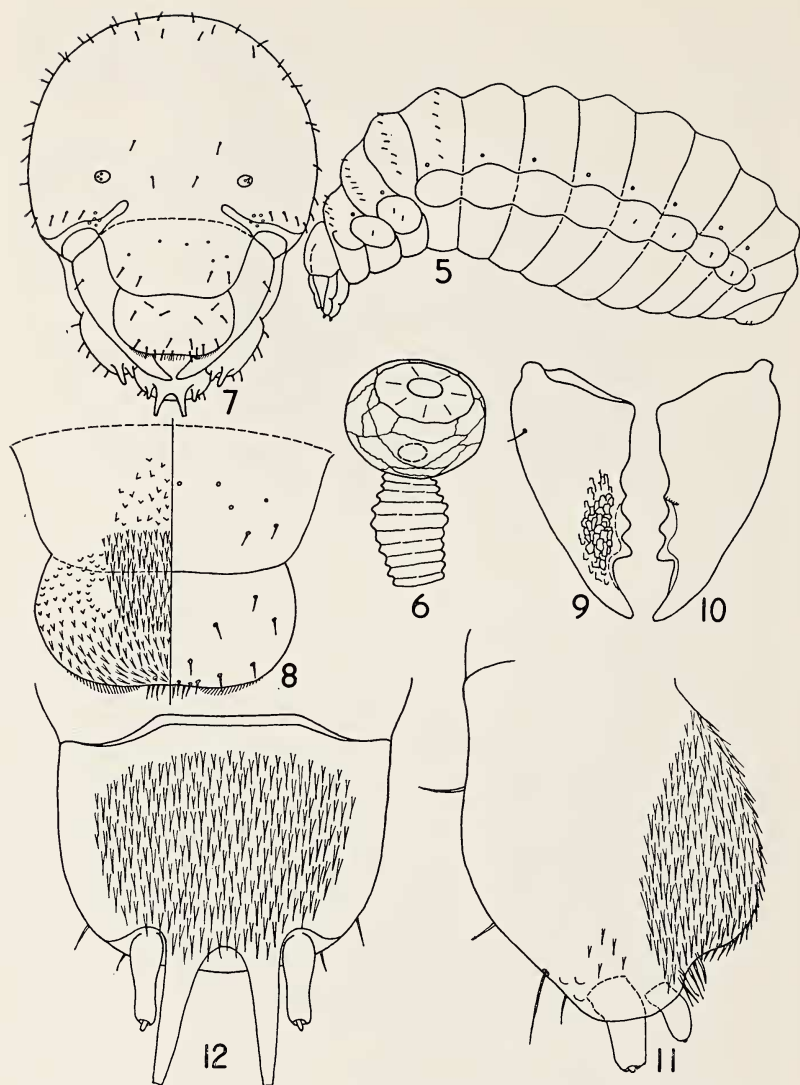
In several nests, cells contained fresh or moldy prey but no egg, larva, or parasites. In three cases, abandoned prey were found buried in the sand plug which sealed off a fully-provisioned cell. Four beetles were entombed in single file in the loose sand in front of a cell containing six prey and an egg. The elytra of one beetle served as a wall-like barrier to the cell.

Egg and Immature Stages. The curved, hyaline egg, 1.5-mm-long, was attached by the cephalic end to the anterolateral mesosternum near one of the procoxae (Fig. 3). It extended transversely but somewhat obliquely across the mesosternum, the free end lying above one of the anterolateral corners of the metasternum. Several mature larvae were reared and are described later in this paper. The brown, ellipsoidal cocoons averaged 2.5×5.5 mm and consisted of silk, saliva, and sand grains (Fig. 4). The uneaten prey fragments were not embedded in the cocoon but were pushed to one end of the cell by the larva.

Nest Repossession and Renovation. During 19-28 August 1970, several females were provisioning nests at Chittenango but no males were seen. Other females were observed searching in holes and crevices rather than bringing in prey. Two of the wasps persisted in entering, backing out of, hovering in front of, and reentering certain burrows. Providing an appropriate site is found, such wasps may repossess and add to nests used earlier in the season by other females. In fact, nest 3 (Fig. 2c) with recently-captured beetles in the burrow also contained a dead *memorialis* female sealed off by loose sand at the end of the main burrow. Cells 1-13 housing cocoons or nearly mature larvae were probably made by the first female before she died, whereas cells 14-20 with recently-captured prey and eggs were probably made by the new occupant. In another nest, containing mostly old cells, a dead *memorialis* female was found deep in the burrow but she was not sealed off with sand. This nest, now being occupied by another female, held some recently completed cells and three beetles in burrow storage.

DESCRIPTION OF THE MATURE LARVA

Six mature larvae from Chittenango which were preserved in Kahle's solution and later transferred to 70% alcohol were utilized in the following description. None of the larvae had begun to spin



Figs. 5-12. Mature larva of *E. memorialis* Banks. 5. Lateral view of entire larva. 6. Thoracic spiracle. 7. Head in frontal view. 8. Clypeus and labrum (right), epipharynx (left). 9. Dorsal view of right mandible. 10. Ventral view of right mandible. 11. Dorsal view of right maxilla. 12. Dorsal view of prementum of labium.

cocoons. Specific parts examined under the microscope were boiled briefly in KOH and then mounted in glycerine.

Body (Fig. 5). Length 7 mm; maximum width 2.5 mm. Stout, slightly curved, fusiform to subclavate, greatest width somewhat beyond middle; pleural lobes prominent, broadly rounded, those on meso- and metathorax oblique and more protuberant; penultimate abdominal segment with small pleural lobe; anus ventral, preapical and directed ventrad, anal segment rounded smoothly beyond anus; integument clothed with abundant minute spinules and sparse setae confined mainly to dorsum and pleural lobes; pronotum, mesonotum and metanotum with transverse series of 12 or 13 setae along dorsal ridge which is free of spinules, thoracic pleural lobes without spinules but with 2 or 3 setae, longest seta on thorax about 58μ ; first abdominal tergite with transverse row of 10 setae, the longest 35μ ; other tergites without conspicuous setae; sternites uniformly and thoroughly clothed with minute spinules; spiracles (Fig. 6) small, weakly pigmented, posterior ones slightly smaller than anterior ones; thoracic spiracular atrium 55μ in diameter, weakly lined with anastomosing non-spinose ridges to form irregular polygons, opening into atrium surrounded by circular, non-sculptured area, entrance to subatrium simple and unarmed.

Head (Fig. 7). Height .80 mm, excluding labrum; width .82 mm. Coronal suture and parietal bands apparently lacking; front with two oval longitudinal impressions between antennal orbits; epistomal suture indistinct, indicated by a weak transverse impression; antennal orbits subcircular, $45\text{--}50 \mu$ in diameter, antennal papillae lacking, three sensilla in equilateral triangle arising from membrane at lateral margin of orbit. Setae on head numerous, 40 of them distributed rather uniformly on sides and top and above bases of mandibles, only 4 setae on frons between antennal orbits, the longest 49μ ; clypeus (Fig. 8) with transverse row of 4 setae and basal transverse series of 7 or 8 minute "sensory" convexities; head weakly pigmented except for anterior tentorial arms and mandibles.

Mouthparts. Labrum (Fig. 8) .39 mm wide, truncate, with about 18 setae 28μ long, distributed laterally and anteriorly, several smaller setae extending from apical margin medially; apical margin bristly except in center; apex of oral surface with median pair of minute sensory pegs arising from circular pores; epipharynx papillose on basal lateral areas but spinulose elsewhere, center with stout, somewhat raised spinules arranged in semicircular pattern; apical

spinules more slender and appressed; small oval area apparently free of pores or sensory structures at each side of central patch of spinules. Mandible (Figs. 9, 10) .41 mm long, .20 mm wide near base, with single basal seta; inner margin with four distinct rounded teeth in about the same plane and decreasing in size from apex to base; basal tooth blunt and transverse; conspicuous, broadly-rounded laminar protuberance between and ventral to second and third teeth; dorsal surface with polygonal sculpturing near teeth.

Maxilla (Fig. 11) strongly and broadly produced mesally, but not angulately so, inner margin densely spinulose, spinules moderately long and appressed; lacinial area with conspicuous tuft of long slender erect spinules; outer margin with four or five strong lateral setae of maximum length 46μ ; palpus 50μ long, stouter than galea which is 28μ long. Hypopharynx a broad lobe with strong dense spinules.

Labium (Fig. 12) with oral surface of prementum completely clothed with moderately long spinules of maximum length 19μ , spinules not separated into patches; base of prementum strongly sclerotized on oral side and separated from remainder of labium by distinct suture; palpi 43μ long, exceeded by paired spinnerets which are 73μ long, spinnerets slender and truncate apically.

DISCUSSION

Entomognathus can be categorized as a genus of chrysolid-hunters, based upon the prey records presented in this paper. Thus far there is no species overlap in the genera of Chrysolidae preyed upon. The European *E. brevis* is the most polyphagous species which has been studied, preying upon no less than 17 species of Alticinae and Cryptocephalinae (Table 1). The North American *E. (Toncahua) texanus* captures galerucine leaf-beetles, whereas *E. (Toncahua) memorialis* preys upon alticine leaf-beetles. One prey species of the latter, *A. ulmi*, has been reported to feed in the field only on *Ulmus americana*, the American elm (Woods, 1918). Nevertheless, we were unable to discover where hunting and prey capture took place. A second prey species, *A. marevagens*, has been collected on *Oenothera biennis*, the evening primrose (J. A. Wilcox, correspondence). The fact that slightly more males than females were taken by *E. memorialis* is puzzling in view of Blatchley's (1910) statement that males of *Altica* are "much less abundant than the females."

The prey of *E. memorialis* is relatively large compared to that of some other crabronine wasps. For example, mean prey/wasp

weight ratios, expressed as decimals, for *E. memorialis*, *Crossocerus maculiclypeus* (Fox), and *Lindeniis columbianus errans* (Fox) were 0.77, 0.22, and 0.07, respectively. This point should not be stressed, however, because the weight of the female wasp may vary depending upon her physical condition (see Iwata, 1942). We caught a female of *Cerceris fumipennis* Say (Sphecidae) at Auburn, N. Y., weighed, released, and recaptured her 12 days later, and found that her body weight had decreased from 95 to 74 mg, or 22%!

Many fully-provisioned cells of *E. memorialis* lacked an egg, larva, or parasites, and we believe this may also be related to the physiological state of the female. Because they were excavated late in the nesting season, such cells were possibly made by females which had already exhausted their egg supplies.

The rather small mean number of prey per cell recorded for *E. memorialis* (5.1) is undoubtedly related to the relatively large mean sizes of the beetles. *E. brevis* constructs a cell of similar size but stores, on the average, considerably more (17.8), usually smaller beetles per cell. There is, in fact, no overlap in the ranges of the number of prey per cell for *brevis* (14-24) and *memorialis* (3-9).

Several other differences in nesting behavior are evident between *brevis* and *memorialis*, particularly in nest structure and dimensions. Projecting turrets have been noted for nests of the former but not for nests of the latter. Series of cells in tandem are common in nests of *memorialis* but have not been observed in nests of *brevis*. The maximum number of cells per nest in *memorialis* (20) is twice as high as that reported for *brevis* (10). The burrows of the former are longer than those of the latter, and the nests are more complicated. Although both species place the egg transversely across the mesosternum of the beetle, the cephalic end is attached mesad to the base of the procoxa in *brevis* (see Fig. II in Grandi, 1927), whereas in *memorialis* it is fastened laterad of the base of the procoxa (Fig. 3). Furthermore, the caudal end of the egg extends beyond the side of the beetle in *brevis* while in *memorialis* it does not.

Several noteworthy similarities in the nesting behaviors of *brevis* and *memorialis* may be applicable for the entire genus. Both species paralyze their prey, probably by stinging, and enter their nests in flight, holding the beetle with the middle legs. The burrow storage of prey observed in *memorialis* is similar to that reported by Maneval (1937) for *brevis*. The burrow-searching adults of *brevis* observed by Adlerz (1912) may play a role similar to that

of the *memorialis* females we implicated in nest repossession and renovation. The egg-bearer is placed venter-up in the cell in both species. The larvae of both species push the uneaten prey remains to one end of the cell rather than distributing them evenly over the surface of the cocoon as in *Lindenius* and certain *Crabro* spp.

A comparison of the mature larva of *brevis*, based upon Grandi's (1927) study, with that of *memorialis* reveals many similarities and only few differences. The base of the prementum of *memorialis* is rather truncate on the oral side, whereas that of *brevis* is strongly rounded. The conspicuous tuft of long, erect setae on the lacinial area of *memorialis* is apparently lacking in *brevis*. The spinules on the inner margin of the maxilla and the oral surface of the prementum of *brevis* are shorter and finer than those of *memorialis*. These differences are seemingly minor and may represent differences in preparation of the material or artistic rendition rather than genuine specific differences.

Our study of *E. memorialis* confirms several behavioral similarities between this genus and the larrine genus *Bothynostethus* which were pointed out in a paper on the nesting behavior of *B. distinctus* Fox by Kurczewski and Evans (1972). The most important of these homologies appear to be transverse, "larrine-like" egg placement and the habit of preying upon adult Chrysomelidae. Other ethological similarities between *E. memorialis* and *B. distinctus* include nesting in sand-cliffs among rootlets, transporting the prey in flight, storing an equivalent number of beetles per cell (mean 5), and placing the egg-bearing prey head-inward and venter-up at the innermost end of the cell.

Several differences in nesting behavior between *E. memorialis* and *B. distinctus* are noteworthy. According to Kurczewski and Evans, *B. distinctus* apparently constructs short branching side burrows from pre-existing galleries made by other insects, resulting in a highly variable nest structure. *E. memorialis* builds undulating, descending burrows with cells in tandem series or clusters around the distal half of the main burrow. Although *B. distinctus* also apparently holds the beetle with the middle legs in flight, it carries the prey dorsum-up and utilizes its mandibles to grasp the beetle's antennae. *E. memorialis* carries the prey venter-up but does not use the mandibles in transport. Burrow storage of prey, a feature typical of many crabronines, has been observed in the latter species and in *E. brevis* but not in *B. distinctus*. The completed cocoon of *Entomognathus* is entirely free of prey remains, whereas that of

B. distinctus contains several beetle elytra firmly embedded at one end.

The mature larvae of *Entomognathus* and *Bothynostethus* have been compared by Kurczewski and Evans (1972). They noted a pair of finger-like lobes on the prothorax, fewer head setae, and three- rather than four-toothed mandibles in *B. distinctus*. It should also be noted that both *E. memorialis* (Fig. 10) and *E. brevis* have in addition to the four teeth along the inner margin of the mandible a conspicuous rounded laminar protuberance ventrad of the second and third teeth. This protuberance is lacking in *B. distinctus*. The maxilla of *B. distinctus* is evenly rounded on the inner margin, whereas that of both *E. memorialis* (Fig. 11) and *E. brevis* (Grandi, 1927) is strongly and broadly produced.

The structural features of the maxilla and mandible of *Entomognathus* tentatively serve to distinguish this genus from all other genera of Sphecidae whose larvae have been described. Our confidence in these characters has been strengthened by comparing recently-collected mature larvae of crabronines in the genera *Lindenius*, *Crossocerus*, and *Anacrabro* with the illustrations and descriptions of species in these genera prepared by Evans (1957, 1959).

In summary, comparison of the European *E. (Entomognathus) brevis* with the North American *E. (Toncahua) memorialis* revealed few significant differences in nesting behavior and substantiated congenerity. Comparing the nesting ethology of the latter crabronine with the larrine *Bothynostethus distinctus* brought to light some striking similarities and rather significant differences.

Differences in the morphology of the mature larvae of species of *Entomognathus* are even more subtle than differences in nesting behavior. Comparison of *E. brevis*, as depicted by Grandi (1927), with *E. memorialis* disclosed few, if any, real differences. The larvae of *Entomognathus* and *Bothynostethus* are, likewise, rather similar and support Evans' (1958, 1959, 1964) belief that the sphecid subfamilies Crabroninae and Larrinae are much more closely related than is currently indicated in the Hymenoptera of America North of Mexico Synoptic Catalog (Muesebeck, *et al.*, 1951; Krombein, 1958; Krombein and Burks, 1967).

The cocoon of *Bothynostethus* is more crabronine than larrine and that of *Entomognathus*, the reverse, based upon comparisons with cocoons of *Lyroda*, *Plenoculus*, *Tachytes*, and *Tachysphex* in the Larrinae and *Lindenius* and certain *Crabro* in the Crabroninae.

ACKNOWLEDGMENTS

We are indebted to J. A. Wilcox, New York State Museum and Science Service, and to A. S. Menke, Systematic Entomology Laboratory, USDA, for identifying the beetles and wasps, respectively. We also thank D. B. Peckham for translating Grandi's (1927) article on *Entomognathus brevis*, D. J. Peckham for photographing the egg attachment and cocoon of *E. memorialis*, and S. and A. Panebianco of Pine Ridge Farms Potatoes, Chittenango, N. Y., for allowing us to utilize their property in our study. E. J. Kurczewski, of Erie, Pa., kindly furnished us with a prey record for *E. memorialis* from Presque Isle St. Pk. Funds, in part, for this study were provided by a Grant-in-Aid from the Research Foundation of the State University of New York (No. 10-7116-A).

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